Reappraisal of some perissodacyl fossils from the Middle Eocene of the Lijiang Basin, Yunnan, China with a revision of tapiroid *Diplolophodon*

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Abstract The Lijiang Fauna from the Lijiang Formation of Lijiang, western Yunnan, was dominated by 13 species of perissodactyl fossils, and its age ranged from Irdinmanhan to Sharamurunian Asian Land Mammal Ages (ALMA) according to previous research. Based on reanalysis of some perissodactyls from the Lijiang Fauna, it is suggested here that *Rhodopagus yunnanensis* is a junior synonym of *Lijiangia zhangi*, which is similar to *Lophiohippus* and placed in Anchilophini within the Palaeotheriidae. The enigmatic and scarce *Lunania* is here regarded as a palaeothere rather than a chalicothere based on its morphological similarities with *Paranchilophus*, and *Lophiohippus* probably represents the upper dentitions of *Lunania*. Furthermore, deperetellid *Diplolophodon* is revised and comprised of three species: *D. similis*, *D. lunanensis*, and *D. xiangshanensis* (comb. nov.). *Teleolophus xiangshanensis* from the Lijiang Formation is reassigned to *Diplolophodon xiangshanensis*. The revised perissodactyls from the Lijiang Fauna are comparable to those from the Rencun Member of the Hedi Formation of the Yuanqu Basin, and its age is confined to Sharamurunian ALMA.

Key words Lijiang Fauna, Yunnan; Middle Eocene; Anchilophini; *Lijiangia*; Deperetellidae; *Diplolophodon*

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1 Introduction

The deposits in the Lijiang Basin of western Yunnan were first referred to the Tertiary “limestone breccia formation” by Misch (1945). Zhao (1965) named the Lijiang Formation for these deposits and suggested its age as the Late Eocene based on the mammal fossils discovered from the top of the Lijiang Formation. Zhao (1965) speculated the lower part of the Lijiang Formation, which is more than a thousand meters in thickness, likely extends to the Early Eocene–Paleocene or even the Cretaceous. Zhang et al. (1978) separated the upper part

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of the Lijiang Formation as the Xiangshan Formation, which varies from 150 to 200 m thick and bears plenty of fossil mammals. However, whether or not the Xiangshan Formation needs to be separated from the Lijiang Formation is still controversial (Zheng et al., 1999; Wang et al., 2021). Furthermore, the Xiangshan Group has been named by Lee et al. (1935) for the Early and Middle Jurassic deposits in Jiangsu and Anhui.

Zong et al. (1996) described the mammal fossils from the Xiangshan Formation in the Lijiang Basin (Fig. 1) and suggested that the age of the Lijiang Fauna is mainly Sharamurunian with some Irdinmanhan taxa. The Lijiang Fauna is composed of 19 species, which are dominated by 13 perissodactyl species including brontothere Metatelmatheriinae gen. et sp. indet., tapiroid *Lophialetes*? sp., *Breviodon lumeiyiensis*, *Teleolophus xiangshanensis*, *Diplolophodon similis*, rhinocerotoid Amynodontidae gen. et sp. indet., *Prohyracodon major*, *P. meridionale*, *Lijiangia zhangi*, *Rhodopagus yunanensis*, chalicothere *Lunania youngi*, *Eomoropus minimus*, and ?*Grangeria cania* (Zong et al., 1996; Wang et al., 2013). These materials are more or less fragmentary and preserved under poor conditions, which can be attributed to the active tectonic movement in the region (Zong et al., 1996). In preparation of the Perissodactyla volume of "Palaeovertebrata Sinica", I noticed some debatable identifications of specimens from the Lijiang Fauna. Here new interpretations of these controversial species are proposed along with a brief discussion of their affinities. Due to the fact that the species reanalyzed in the present paper have already been described in detail by Zong et al. (1996) and Huang (1999), this paper focuses on their validities and affinities.

Fig. 1 Paleogene mammal fossil localities in the Yunnan Province (modified from GS(2017)1267)

2 Methods

The specimen IVPP V 9901, V 12471, and V 9903 were scanned using a GE v|tome|x m300&180 micro-computed-tomography scanner (GE Measurement & Control, Wuntsdorf, Germany) that is housed at the Key Laboratory of Vertebrate Evolution and Human Origin of Chinese Academy of Sciences. The data sets have resolutions of 24.538 μm (for V 9901) and 28.935 μm (for V 12471, V 9903), and the scans were carried out at 140 kV and 140 or 120 μA. Two frames per projection were acquired by a timing of 1000 ms for a total of 1800 projections. The 3D virtual models were reconstructed by VGStudio Max (version 3.2).

The dental terminology follows Dashzeveg and Hooker (1997), which essentially follows Hooker (1989, 1994). It is necessary to mention that the protostylid, as used by Dashzeveg and Hooker (1997), is a crest labial to the protoconid and raising from the cingulid at the ectoflexid, and the posthypocristid is a short crest extending posteriorly from the hypoconid.

Institutional abbreviations GMC, Geological Museum of China, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PMUM, Museum of Evolution (Paleontological Museum), Uppsala University, Uppsala, Sweden; SDM, Shandong Museum, Ji'nan, China.

3 Taxonomic revision of some perissodactyls

Order Perissodactyla Owen, 1948

Superfamily Equoidea Hay, 1902

Family Palaeotheriidae Bonaparte, 1850

Subfamily Pachynolophinae Pavlow, 1888

Tribe Anchilophini Remy, 2012

Genus *Lijiangia* Zong et al., 1996

Type and only species *Lijiangia zhangi* Zong et al., 1996.

Type locality and horizon Loc. 83009, Xiangshan, Lijiang, Yunnan; Lijiang Formation.

Diagnosis P3–4 unmolariform, P4 with distinct paracone rib and low, weak metaconule; upper molars with rib-shaped parastyles, long postmetacristae, probable well-developed metastyle on M3, and strongly oblique metaloph, which joins the midpoint between the paracone and metacone. Differs from *Lophiohippus* by a smaller size (M1–2 length about 19.2% shorter), a less compressed and shorter parastyle on M1–3, and slightly more concave ectoloph on M1–2.

***Lijiangia zhangi* Zong et al., 1996**

(Fig. 2)

Rhodopagus yunnanensis Zong et al., 1996, p. 94, fig. 2-6, 2-7, pl. 33, 5–7

Holotype IVPP V 9908, a right maxilla with P4–M2 and P3 root.

Referred specimens IVPP V 9909, a left maxilla with DP2–4 and M1; V 9909.1, a left maxilla with broken M1 and M2; V 9909.2, a right M3; V 9909.3, a left M1/2. All material

from Loc. 83009, the Lijiang Formation of Lijiang Basin.

Type locality and horizon Xiangshan of Lijiang, Yunnan; Lijiang Formation.

Discussion The holotype of *Lijiangia zhangi* (IVPP V 9908) is a fragmentary maxilla with P4–M3 (Fig. 2A). The M1 is heavily worn and the crown has many small cracks, which contributes to its relatively larger size. The M2 is moderately worn and nearly undeformed, but both the paracone and parastyle are broken. Therefore, it is uncertain whether or not the M2 parastyle is overlapped by the M1 metastyle, which is not the case in other tapiromorphs. Although the metastyle of the P4 partially overlaps the parastyle of the M1, the P4 is not completely erupted. It is doubtful that the condition would remain same after the P4 is completely erupted, because a small metastyle of the P4 unlikely overlaps a relatively larger M1 parastyle. As a result, two main diagnosis characters of *Lijiangia* as proposed by Zong et al. (1996), the M1 considerably larger than the M2 and the parastyle overlapped by metastyle of the preceding tooth, cannot be confirmed based on the preserved condition of the specimen. On the other hand, the specimen is characterized by a rib-shaped parastyle, a strongly oblique metaloph joining the midpoint between the paracone and metacone, and a long postmetacrista on M1–2.

Zong et al. (1996) also reported a new species *Rhodopagus yunnanensis* from the Lijiang Formation at locality 83009 where *Lijiangia* was discovered. The material of *R. yunnanensis* comprises a left maxilla with DP2–4 and the M1 (IVPP V 9909, holotype) (Fig. 2B), a left maxilla with the M2 and broken M1 (V 9909.1) (Fig. 2C), a left M1/2 (V 9909.3) (Fig. 2D), and a right M3 (V 9909.2) rather than the M2 (Fig. 2E) as originally assigned. The V 9909.2 has a relatively more lingually depressed metacone and a probable more distinct, labially deflected metastyle with a convex basal posterior border than on the M1 and M2, so it is more likely to be the M3 than the M1 or M2. Zong et al. (1996) considered that *R. yunnanensis* is similar to *R. minimus* (=*R. pygmaeus*) in morphology, but is relatively larger, has a parastyle rib that is more labially protruded, the paracone and parastyle are more convex, and the metacone and metastyle (i.e. longer postmetacrista) are longer on the upper molars. In addition, *R. yunnanensis* differs further from *R. minimus* in having more oblique metalophs on M1–3 and probably a labially deflected metastyle on the M3. The long postmetacrista on M1–2 of *R. yunnanensis* is also characterized by those of *Lijiangia*. Furthermore, the metaloph is strongly oblique and joins the ectoloph between the paracone and metacone on M1–2 in both species. The slightly worn M1/2 (V 9909.3) and M3 (V 9909.2) of *R. yunnanensis* show that the metaloph oriented towards the parastyle and then curves to the midpoint between the paracone and metacone. The two species are also very similar in size and from the same locality. The M1 of *R. yunnanensis* has a more prominent paracone rib and parastyle rib than that of *Lijiangia*, but the difference can be attributed to a lesser degree of wear in the former. As a result, *Rhodopagus yunnanensis* is regarded as a junior synonym of *Lijiangia zhangi*. The M3 of '*Rhodopagus*' *yunnanensis* indicates the probable presence of a well-developed, labially deflected metastyle in *Lijiangia*.

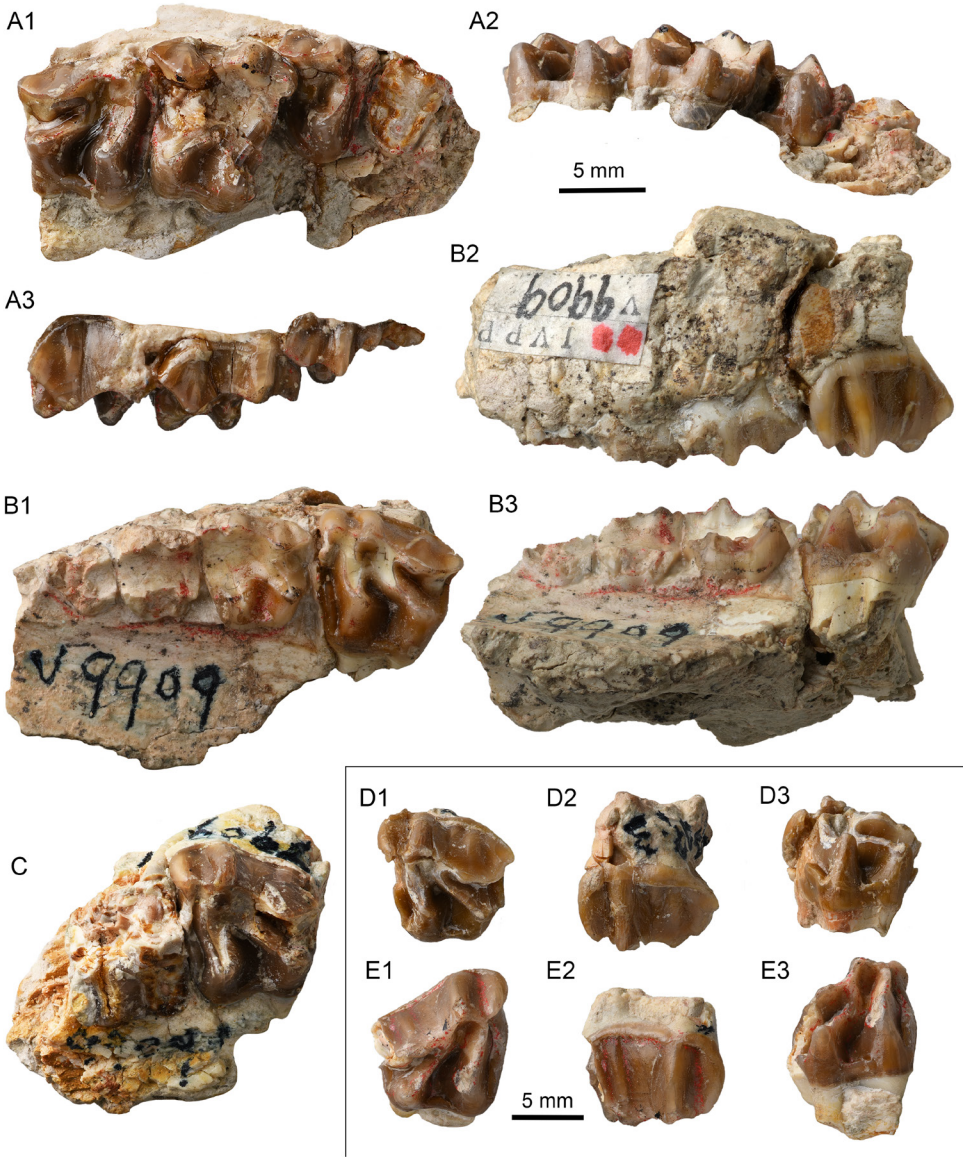

Fig. 2 Maxillae and upper molars of *Lijiangia zhangi* from the Lijiang Formation of Lijiang Basin, Yunnan
A. right maxilla with P4–M2 (IVPP V 9908, holotype) in occlusal (A1), lingual (A2), and labial (A3) views;
B. left maxilla with DP2–DP4 and M1 (V 9909, holotype of '*Rhodopagus yunnanensis*') in occlusal (B1), labial (B2), and lingual (B3) views; C. left maxilla with broken M1 and M2 (V 9909.1) in occlusal view;
D. left M1/2 (V 9909.3) in occlusal (D1), labial (D2), and lingual (D3) views;
E. right M3 (V 9909.2) in occlusal (E1), labial (E2), and lingual (E3) views

Huang and Wang (2001) uncertainly assigned two isolated upper and lower molars (IVPP V 12468, 12469) to ?*Rhodopagus yunnanensis* from the Hedi Formation of the Yuanqu Basin, Shanxi. However, they are closer to *Yimengia* than to *Rhodopagus* or *Lijiangia* in having a moderately long postmetacristia and less oblique metaloph on the upper molar, as well as a transversely extended protolophid and distinct cristid obliqua on the lower molar (Bai et al., 2020).

Huang and Qi (1982) reported a new species *Lophialetes yunnanensis* from the Lunan Basin in Yunnan Province. Bai (2017) pointed out its affinity with European anchilophins and erected a new genus *Lophiohippus* for the species. Although *Lophiohippus* is only known by a maxilla with three molars, it is similar to *Lijiangia* in having a rib-like paracone and parastyle, long postmetacrista, strongly oblique metaloph, and in that the M3 metastyle was probably labially deflected. *Lophiohippus* differs from *Lijiangia* in its larger size, by having a more compressed parastyle which seems more separated from the paracone, and in having a slightly convex labial surface of the ectoloph on M1–2. Whether or not the parastyle overlaps the metastyle of the preceding teeth, which is a diagnostic character in *Lophiohippus*, is uncertain in *Lijiangia*. However, determining whether or not the differences between *Lophiohippus* and *Lijiangia* are at the generic level depends on the discoveries of more complete specimens. Bai (2017) assigned *Lophiohippus* to Anchilophini and suggested that it is closer to *Paranchilophus* than to *Anchilophus*. Because M1–3 of *Lijiangia* is similar to that of *Lophiohippus*, it is more logical to assign *Lijiangia* in Anchilophini rather than the ?Hyracodontidae as initially placed. Thus, both *Lophiohippus* and *Lijiangia* represent palaeothere anchilophins in the Middle Eocene of Asia, indicating sporadic communications between Asia and Europe during the Middle Eocene (Bai, 2017).

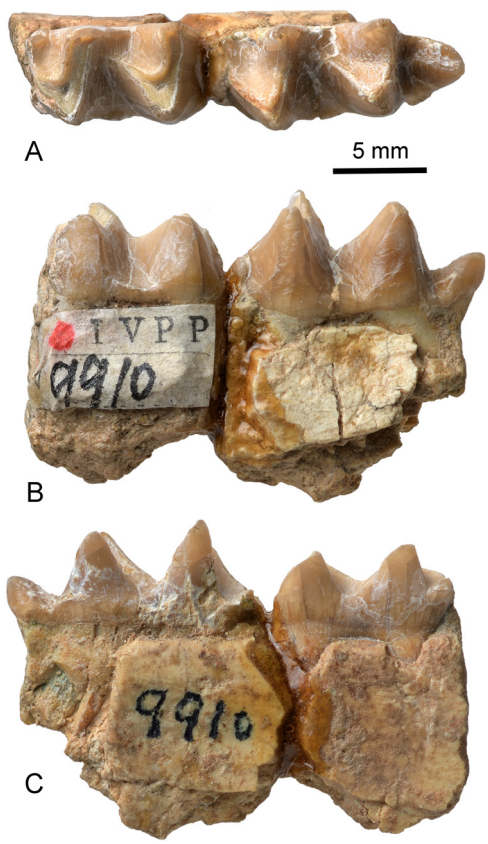

Fig. 3 Left mandible of *Lunania youngi* (IVPP V 9910) from the Lijiang Formation of the Lijiang Basin, Yunnan, in occlusal (A), labial (B), and lingual (C) views

The recognition of *Lijiangia* and *Lophiohippus* as palaeotheres also illuminate the affinity of *Lunania*. The enigmatic *Lunania* comprises two species: *L. youngi* from the Lunan and Lijiang Basin of Yunnan (Chow, 1957; Zong et al., 1996) (Fig. 3) and *L. zhoui* from Yuanqu Basin of Shanxi (Huang, 2002). Chow (1957) initially assigned *Lunania* to the Lophiodontidae based on its general lophiodont teeth and a looped hypoconulid on the m3. Chow (1962) suggested a relationship of *Lunania* with chalicotheres and noticed its similarities with chalicothere *Eomoropus ulterior* from the Lunan Basin in having a transversely extended protolophid and hypolophid, anterolingually directed paralophid and cristid obliqua, and a cleft-like depression on the lingual side of the hypoconulid. However, *Lunania* differs from *Eomoropus* and other chalicotheres in lacking the twinned metaconids

on the lower molars as pointed out by Chow (1962). On the other hand, *Lunania* shows some similarities with palaeothere *Paranchilophus* in lacking twinned metaconids on the lower molars, in having small hypoconulid on m1–2, and a relatively small size and high hyposodont (Remy, 2012). The lower molars of *Paranchilophus* differ from those of *Lunania* by having a higher paralophid and cristid obliqua, a rounded crescent of trigonid and/or talonid, and a much more oblique protolophid and hypolophid (Remy, 2012). It is likely that the holotype of *Lophiohippus* represents the upper molars of *Lunania*, which is known only from the lower molars. Both *Lophiohippus* and *Lunania* are certainly from the Lumeiyi Formation (Russell and Zhai, 1987), nearly the same in size (m1–3 length of *Lunania* 31.6 mm; M1–3 length of *Lophiohippus* 33.4 mm), and show similarities in morphologies with *Paranchilophus*. Thus, *Lophiohippus* has to be regarded as a junior synonym of *Lunania* if their association is proved by more complete specimens in the future.

Superfamily Tapiroidea

Family Deperetellidae Radinsky, 1965

Genus *Diplolophodon* Zdansky, 1930

Type species *Diplolophodon similis* Zdansky, 1930.

Diagnosis (modified from Ding et al., 1977) Small deperetellid; premolar series nearly as long as or slightly shorter than molar series; premolars with high degree of molariform, P2 relatively short and wide, P2–4 protoloph nearly parallel to the metaloph; M1–3 with prominent posterolabial cingulum, short postmetacrista, and lack of the lingual cingulum; lower canine relatively small; postcanine diastema short; p1 small with a single root; p1–2 not elongated; p2 with a low hypolophid, p3–4 with complete hypolophid; lower molars bilophodont, labial cingulids weak or absent, and lack of lingual cingulids. Differs from *Deperetella* and *Bahinolophus* by a much smaller size, and P2 more rectangular in outline with the protoloph nearly parallel to the metaloph. Further differs from *Deperetella* by shorter premolar series than molar series, more distinct postmetacrista on the upper molars without lingual cingula, a single root of p1, a much shorter p2, p2–4 with distinct protostylid, and lower cheek teeth lack of well-developed labial cingulids. Further differs from *Bahinolophus* by a flatter ectoloph on P3, a shorter, more lingually appressed postmetacrista on M1–2, straighter protoloph and metaloph on the upper molars with more distinct posterolabial cingula, a more distinct hypolophid on p2, and lack of crista on the lingual side of the paracone and a crest on the labial side of the ectoloph on M1–2.

Included species *D. similis*, *D. lunanensis*, and *D. xiangshanensis* (comb. nov.).

Diplolophodon similis Zdansky, 1930

(Figs. 4–5; Table 1)

Diplolophodon similis Young, 1937, p. 419, fig. 5

Diplolophodon major Young, 1937, p. 421, fig. 6

Deperetella similis Radinsky, 1965, p. 226 (part)

Diplolophodon cf. *D. similis* Ding et al., 1977, p. 38, pl. 1, fig. 4

Diplolophodon qufuensis Shi, 1989, p. 91, pl. 1, fig. 7

Lophialetes? sp. Zong et al., 1996, p. 80, pl. 32, fig. 1

Diplolophodon similis Zong et al., 1996, p. 83, pl. 32, fig. 4

Teleolophus cf. *T. xiangshanensis* Huang and Wang, 2001, p. 198, pl. 1, fig. 4

Holotype PMUM 3440, a right maxilla with lingual part of P3, and P4–M3.

Referred specimen IVPP V 5103, a fragmentary lower jaw with left p3–4 and m3, Dongjun Formation, Bose, Guangxi; SDM 84008, a left mandible with p4–m3, Guanzhuang Formation, Qufu, Shandong; IVPP V 9904, 9904.1–7, isolated upper and lower cheek teeth, a right mandible with m2–3, V 9901, a left mandible with p2–4, Loc. 83009, Lijiang Formation, Lijiang, Yunnan; IVPP RV 37105, a left maxilla with P2–4, V 12471, a right mandible with dp3 talonid and dp4, Hedi Formation, Yuanqu, Shanxi.

Type locality and horizon Lok. 7, Mianchi, Yuanqu Basin, Hedi Formation.

Diagnosis P4 with a concave, lingually appressed metacone and protoloph joining the ectoloph; p3 with a high cristid obliqua and a distinct posthypocristid; p4 with an anterolingually extended cristid obliqua and a distinct posthypocristid; labial cingulid well-developed at the base of ectoflexid on p2–4, forming the crestiform protostylid; lower molars relatively narrow.

Discussion The holotype of *Diplolophodon similis* is only known by a maxilla with P3–M3 from the Lok. 7 of Mianchi in Henan (Zdansky, 1930). Young (1937) assigned a maxilla with P2–4 to the species and erected a new species *D. major* from Yuanqu of Shanxi, which is located on the opposite bank of the Lok. 7. Radinsky (1965) suggested that *D. major* is a junior synonym of *D. similis*, and *Diplolophodon* is synonymous of *Deperetella*. Chow et al. (1974), in agreement with Radinsky (1965), placed two maxillae with P3–4 and three mandibles with lower cheek teeth to *Deperetella similis* discovered from the Shilin (Lunan) of Yunnan. However, Ding et al. (1977) still considered *Diplolophodon* as a valid genus and assigned a lower jaw with p3–4 and the m3 to *Diplolophodon* cf. *D. similis* from the Dongjun Formation of the Bose Basin, Guangxi. Zong et al. (1996) assigned isolated cheek teeth and a mandible with m2–3 (IVPP V 9904, 9904.1–7) to *Diplolophodon similis* from the Lijiang Formation of Yunnan. Jin and Seo (2001) erected a new species *Diplolophodon lunanensis* based on the Shilin specimens described by Chow et al. (1974); they also assigned *D. similis* from Lijiang and *Diplolophodon* cf. *D. similis* from Bose to *Diplolophodon* cf. *D. lunanensis*. In contrast, Dashzeveg and Hooker (1997) and Tsubamoto et al. (2005) still considered *Diplolophodon* to be a junior synonym of *Deperetella*. Tsubamoto et al. (2000) even synonymized all species of *Diplolophodon* from China with *Deperetella birmanica*, however, Tsubamoto et al. (2005) erected a new genus *Bahinolophus* for the species *B. birmanicus* from Myanmar. As pointed out by Ding et al. (1977), the ratio of the lower premolar length to molar lengths in *Diplolophodon similis* is 0.9, while that of *Deperetella cristata* is 1.13; *Diplolophodon* further differs from *Deperetella* by a relatively smaller canine, the single root of the p1, p1–2 not being elongated, the P2 being shorter and wider with the protoloph more parallel to the

metaloph, and that the M1–3 posterolabial cingula are more prominent and lack of lingual cingula (Radinsky, 1965; Ding et al., 1977). Thus, *Diplolophodon* is a valid genus, and the species *D. similis* is different from *Deperetella cristata* at the generic level.

Here, it is agreed that Shilin specimens represent a new species *Diplolophodon lunanensis*, which is mainly characterized by a flat and straight ectoloph on P3–4, a prominent paraconule on the P3, a cristid obliqua developed and distinct cristid posterior to the hypoconid on the p3, and a p4 that is relatively short and wide as pointed out by Jin and Seo (2001). The P4 of Shilin material further differs from that of *D. similis* by the protoloph dying out before reaching the ectoloph.

Zong et al. (1996) assinged isolated cheek teeth and a mandible with m2–3 (V 9904, 9904.1–7) to *D. similis* from the Lijiang Formation of Yunnan. The P3 (V 9904.3) and M2–3 of Lijiang material are generally similar to those of holotype of *D. similis*, but the former lacks the lingual cingulum on the P3 and a postmetacrista on the M3, as well as has a less distinct posterolabial cingula (metastyle) on M2–3. However, these differences could be attributed to intraspecific variation. The Lijiang material are narrower (m2 length-width ratio 1.22) than those of *D. lunanensis* (m2 length-width ratio 1.01), and the P3 of former lacks a distinct paraconule. The material from Lijiang is therefore more reasonably assigned to *D. similis* than to *Diplolophodon* cf. *D. lunanensis*. Unfortunately, the lower premolars were not preserved in any reported *D. similis* from Lijiang.

Zong et al. (1996) reported a mandible with dp3–m1 (V 9901) to *Lophialetes*? sp. (Fig. 4A) from the Loc. 83009 where the Lijiang specimens of *D. similis* were found. However, the preserved three teeth are indeed p2–4 as clearly shown by CT image (Fig. 4A4), and their high degrees of molariform along with their small sizes indicate that the mandible is different from *Lophialetes* and more likely represents *Diplolophodon*. Considering *D. similis* has been also reported from the same locality, I tentatively assign the mandible with p2–4 to *D. similis*. The p3 of V 9901 is similar to that of *D. lunanensis* in having a high cristid obliqua joining the protoconid in a high position, and the former has a short crest (posthypocristid) descending posteriorly from the hypoconid, which is also discernable in V 31 of *D. lunanensis*. The p4 of V 9901 differs from that of *D. lunanensis* by a more lingually directed cristid obliqua. Whether or not the posthypocristid is also present on the p4 as in the p3 is uncertain in V 9901 due to the breakage, but the posthypocristid of the p4 varies from discernable to absent in *D. lunanensis*. In addition, p2–4 of V 9901 have a well-developed, raising crestiform cingulid at the base of the ectoflexid, forming the protostylid as named by Dashzeveg and Hooker (1997), while the labial cingulids vary from absent to weak on p3–4 in the specimens of *D. lunanensis*. The p4 of *D. lunanensis* shows some other variations: one mandible of V 31 has a much weaker cristid obliqua and relatively wider talonid than in the other two specimens.

Huang and Wang (2001) reported a mandible with m1–2 (IVPP V 12471) from the Yuanqu Basin (Fig. 4B) and tentatively assigned it to *Teleolophus* cf. *T. xiangshanensis* based mainly on the small size and bilophodonty. However, CT images show that tooth germs are

present beneath the teeth, indicating a mandible with dp3–dp4 rather than m1–2. The p3–4 are not complete, and the p4 is deformed with the occlusal surface somewhat towards the lingual side (Fig. 4B3). The preserved part of the p3 (Fig. 4C–D) has a well-developed protolophid and hypolophid, a high cristid obliqua joining the protoconid, a distinct paralophid, and a short posthypocristid. The preserved p4 (Fig.4D–E) also has a well-developed protolophid and hypolophid, but differs from the p3 in having more rounded angles at the protoconid, a lower cristid obliqua descending towards the protolophid, and a longer, more distinct posthypocristid. The p3–4 of V 12471 shows some similarities with that of V 9901, but differs from that of *D.*

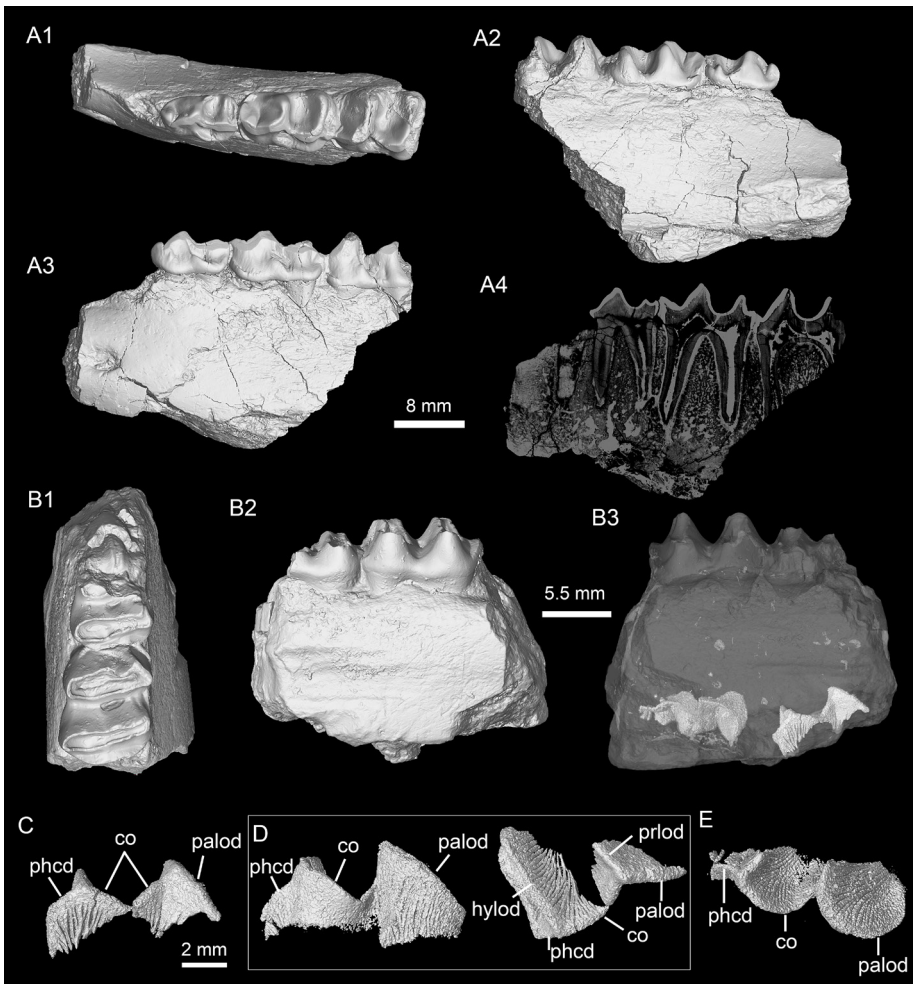

Fig. 4 Mandibles of *Diplolophodon similis*

A. Left mandible with p2–4 (IVPP V 9901) from the Lijiang Formation of Lijiang Basin, Yunnan, in occlusal (A1), lingual (A2), labial (A3), and longitudinal section (A4) views; B–E. right mandible with talonid of the dp3, dp4, and developing p3–4 in the socket (V 12471) from the Hedi Formation of Yuanqu Basin, Shanxi: B. mandible with dp3–4 in occlusal (B1), lingual (B2), and labial (B3) views with p3–4 in the socket; C. labial view of p3; D. occlusal view of the p3 and labial view of the p4 *in situ*; E. occlusal view of the p4
Abbreviations: co. cristid obliqua; hylod. hypolophid; palod. paralophid; phcd. posthypocristid; prlod. protolophid

lunanensis, in having a cristid obliqua more lingually extended on the p4. V 12471 is more reasonably assigned to *D. similis* than to other species of *Diplolophdon* based on its general morphology, size, and locality. Furthermore, the posthypocristid of the p4 (unknown on the p3), which was considered to be a characteristic in *Bahinolophus birmanicus* from the Middle Eocene of Myanmar, is also present in *D. similis* and some specimens of *D. lunanensis* (Colbert, 1938; Radinsky, 1965; Tsubamoto et al., 2005).

Table 1 Measurements of *Diplolophodon similis*, *D. lunanensis*, and *D. xiangshanensis* (mm)

		D. similis						*D. lunanensis*			*D. xiang*
		PMUM 3440	RV 37105	V 9904, 9904.1, 3	V 9904.4*	V 5103*	SDM 84008*	GMC V 29 (Left)	GMC V 31*	GMC V 713*	V 9903, 9903.1*
P1/p1	L								4.5#		
	W								4#		
	L/W								1.13		
P2/p2	L		9.0			9			9#		
	W		10.8			5			5.2#		
	L/W		0.83			1.80#			1.73#		
P3/p3/dp3	L	9.0#	9.0	9.7		12		10	12.8		11.5
	W	11.5#	12.3	11.9		7.5#		12.8	8.1		6.8
	L/W	0.78#	0.73	0.82		1.60#		0.78	1.58		1.69
P4/p4/dp4	L	9.4	9.5			10.5	11.3	10.7	11.7	10.9	10.0
	W	13.4	13.0			8.5	8.0	14.3	10.0	10.4	8.0
	L/W	0.70	0.73			1.24	1.41	0.75	1.17	1.05	1.25
P1–4/p1–4	L					36.1			38.0		
P2–4/p2–4	L		27.5			31.5			33.5		
P3–4/p3–4/dp3–4	L	18.4#	18.5			22.5		20.7	24.5		21.5
M1/m1	L	10.5			13.0	12.5	13.0			11.4	10.5
	W	14.0#				9.5#	9.6			11.5	9.2
	L/W	0.75#				1.32#	1.35			0.99	1.14
M2/m2	L	12.5		14.4	14.0	13	15.0			13.8	11.8
	W	15.5#		16.3	11.5	11.5#	10.9			13.6	9.0
	L/W	0.81#		0.88	1.22	1.13#	1.38			1.01	1.31
M3/m3	L	13.0		14.2	15.8	14.1				16.4	
	W	16.4		16.7	12.0	11.8				13.3#	
	L/W	0.79		0.85	1.32	1.19				1.23#	
M1–3/m1–3	L	35.5			41.7	39.6				40.6	

Note: Measurements of lower teeth are indicated by the asterisks after specimen numbers. The measurements of *D. xiangshanensis* are from dp3–dp4 and m1–2; numbers with superscript "#"mean approximate values. GMC V 31 and V 713 were remeasured, while other measurements of specimens are from Zdansky (1930), Young (1937), Ding et al. (1977), Shi (1989) and Zong et al. (1996).

Ding et al. (1977) reported a fragmentary lower jaw with left p3–4 and m3 (IVPP V 5103) of *Diplolophodon* cf. *D. similis* from the Dongjun Formation of the Bose Basin, Guangxi. Ding et al. (1977) pointed out that the size and morphology of V 5103 are similar to those of *D. similis* from Shilin, but the former has relatively narrower teeth and slightly more distinct posterior cingulids on p3–4. The posterior cingulid on p3–4 is too damaged to confirm its condition. In addition, p3–4 of V 5103 is similar to that of *D. similis* in having a relatively distinct paralophid and cristid obliqua, a high cristid obliqua on the p3, and a more lingually extended cristid obliqua on the p4. Thus, I suggest assigning V 5103 to *D. similis*.

Shi (1989) reported a new species *Diplolophodon qufuensis* based on a mandible with p4–m3 (Fig. 5) from the Huangzhuang Formation in Qufu of Shandong. According to Shi (1989), *D. qufuensis* was diagnosed by its large size, the straight lower border of the horizontal ramus, a parallel protolophid and hypolophid, relatively narrow check teeth, a complete hypolophid on the p4, and the absence of labial and lingual cingulids on the lower molars. However, many of these characters are common in *Diplolophodon*, and only two characters seem valid: a large size and relatively narrow check teeth. The size of *D. qufuensis* is close to that of *D. similis* (V 9904 and V 5103), and its m2 length-width ratio is 1.38, which is slightly greater than that of *D. similis*. In addition, the p4 has an anterolingually directed cristid obliqua and a crestiform protostylid as in *D. similis*. *Diplolophodon qufuensis* is therefore considered to be a junior synonym of *D. similis* as proposed by Zong et al. (1996).

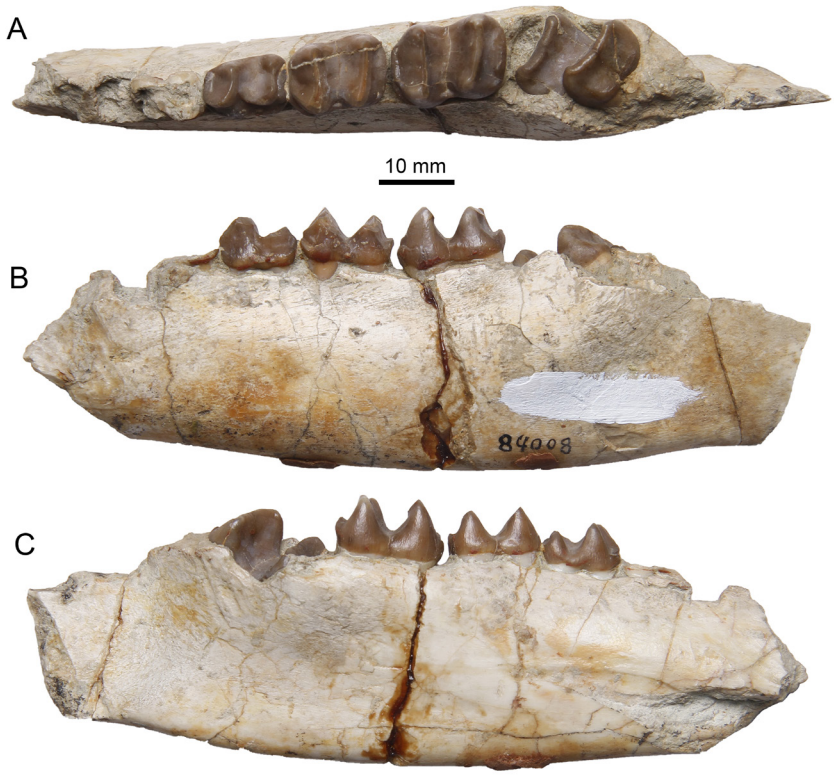

Fig. 5 Left mandible of *Diplolophodon similis* (=*D. qufuensis*, holotype, SDM 84008) from the Huangzhuang Formation of Qufu, Shandong, in occlusal (A), labial (B), and lingual (C) views

***Diplolophodon lunanensis* Jin & Seo, 2001**

(Table 1)

Deperetella similis Chow et al., 1974, p. 263, pl. 1, figs. 3, 5–7

Holotype GMC V 29, left and right maxillae with P3–4.

Paratypes GMC V 31, two left mandibles with p3–4 and the dp3, p4; GMC V 713, a right mandible with the p3 talonid and p4–m3.

Type locality and horizon Lunan Basin, Yunnan; Lumeiyi Formation.

Diagnosis (modified from Jin and Seo, 2001) Paraconule of P3 distinct; P4 with a flat ectoloph, less separated parastyle, and protoloph dying out before reaching the ectoloph; p3 with a high cristid obliqua, and distinct protostylid and posthypocristid; p4 relatively wide and cristid obliqua anteriorly directed; lower molars relatively wide.

Comments All materials of *D. lunanensis* were reported from the Lumeiyi Formation near Banqiao of Shilin. It is necessary to mention that the holotype and GMC V 31 were found from Xiaoshahe, while GMC V 713 was found from Dakexiang (Chow et al., 1974).

Diplolophodon xiangshanensis (Zong et al., 1996)

(Fig. 6; Table 1)

Teleolophus xiangshanensis Zong et al., 1996, p. 82, figs. 2-3, pl. 32, fig. 3.

Holotype IVPP V 9903, a right mandible with dp3–4, m1, and talonid of dp2.

Referred specimen IVPP V 9903.1, a right m2.

Type locality and horizon Loc. 83009, Xiangshan, Lijiang Basin, Yunnan; Lijiang Formation.

Diagnosis Small *Diplolophodon* (m1 length 10.5 mm); weak labial cingulids on lower molars; lower molar relatively narrower than in *D. lunanensis*.

Discussion Zong et al. (1996) erected a new species *Teleolophus xiangshanensis* based on a mandible (IVPP V 9903) that preserves three lower teeth interpreted as dp4–m2 (Fig. 6A–D), although Zong et al. (1996) mentioned that no teeth are discernable in the socket. Zong et al. (1996) assigned the species to *Teleolophus* based on its small size, a weak labial cingulid on the lower molars, and the presence of cement. The CT image shows that beneath the teeth there are no tooth germs (Fig. 6E). However, the roots are relatively open between the tips (beyond the anterior and posterior borders of crown) in the anterior two teeth indicating that these teeth are deciduous. Furthermore, the preserved ultimate tooth is nearly unworn, whereas the anterior two teeth are moderately worn to a similar degree. Thus, the preserved ultimate tooth erupted later than the anterior two teeth, which suggests that the three preserved teeth are more reasonably interpreted as dp3–dp4 and the m1. In addition, the preserved anterior most tooth is rather elongated with three transverse lophids, which is a feature of the dp3 in some tapiroids (Radinsky, 1965). Thus, the teeth of this mandible are actually dp3–m1 instead of dp4–m2. The dp4 is completely molarized, and its morphology is the same as that of the m1 in having a transversely extended, parallel protolophid and hypolophid. In addition, cement is present in the talonids of dp3–4, while it is lacking in the talonid of the m1. Considering that the bilophodont m1–2 are relatively small size, the mandible is more reasonably assigned to *Diplolophodon* than to *Teleolophus*. The holotype of *D. xiangshanensis* differs from mandibles of the other two species of *Diplolophdon* in having a smaller size, relatively narrower lower cheek teeth (compared to *D. lunanensis*), cement in the talonids of dp3–4, and incomplete labial cingulids on the lower molars. Huang and Wang (2001) reported a mandible with dp3–4 instead of m1–2 (IVPP V 12471) from the Yuanqu Basin and tentatively assigned it

to *Teleolophus* cf. *T. xiangshanensis* based mainly on the small size and bilophodonty. This specimen differs from *D. xiangshanensis* in its lack of cement on dp3–4 and has been assigned to *D. similis* as discussed above.

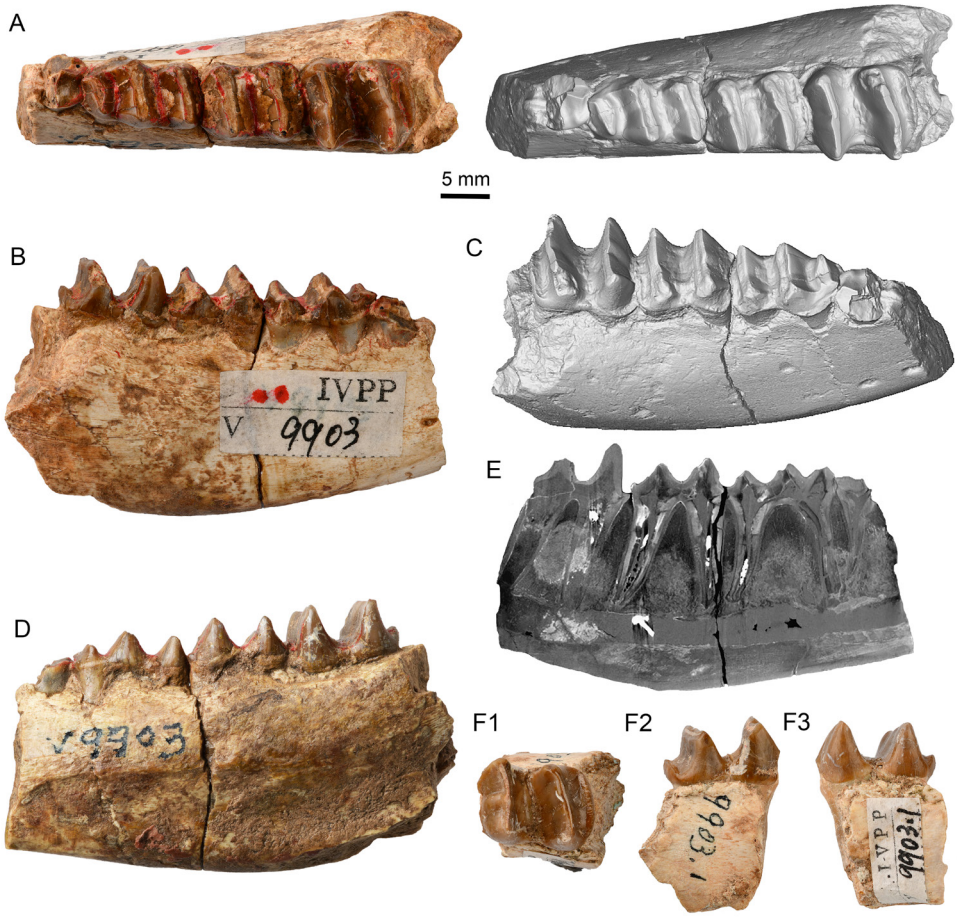

Fig. 6 *Diplolophodon xiangshanensis* from the Lijiang Formation of Lijiang Basin, Yunnan
A–E. mandible with dp3–m1 and talonid of dp2 (IVPP V 9903, holotype)
in occlusal (A), labial (B), occlusolabial (C), lingual (D), and longitudinal section (E) views;
F. right m2 (V 9903.1) in occlusal (F1), labial (F2), and lingual (F3) views

4 The age of Lijiang Fauna

Zong et al. (1996) and Huang (1999) correlated the Lijiang Fauna to the corresponding faunas from the upper part of Lumeiyi Formation of Shilin, the Rencun member of Hedi Formation of Yuanqu, and the Huangzhuang Formation of Qufu. The age of Lijiang Fauna is considered to be ranging from Irdinmanhan to Sharamurunian Asian Land Mammal Ages (Zong et al., 1996; Wang et al., 2021). In terms of revised perissodactyls from the Lijiang Fauna, they are comparable to those from the Rencun member of the Hedi Formation. Four species and two genera are shared between the two faunas: *Diplolophodon similis*, *Prohyracodon meridionale*,

Eomoropus minimus, *Grangeria canina*, *Breviodon* and *Lunania* (Huang and Wang, 2001; Huang et al., 2001; Huang, 2002). Three species of the Lijiang Fauna are also reported from the Lumeiyi Formation with certainty: *Lunania youngi* from the lower part discovered from the nearby locality of Shilin and *Diplolophodon similis*, *Prohyracodon meridionale* from the upper part of the localities south of Banqiao (Zhang et al., 1978; Zheng et al., 1978; Russell and Zhai, 1987). Only two species are shared between the Lijiang Fauna and Huangzhuang Fauna: *Diplolophodon similis* and *Eomoropus minimus* (Shi, 1989). Here, it is proposed that the age of Lijiang Fauna be restricted to Sharamurunian based on the following evidence: 1) Specimens of *Lophialetes* and *Teleolophus* from the Lijiang Fauna, which are typical elements of Irdinmanhan fauna, are considered to be misidentified and reassigned to *Diplolophodon*; only the genus *Breviodon* is shared with Irdinmanhan mammals (Bai et al., 2018); 2) The premolars of *Diplolophodon* from the Lijiang Fauna has a high molariform degree as seen in *Deperetella*, which is a typical element of Sharamurunian fauna; 3) The perissodactyls from Lijiang are comparable to those from the Rencun Member of the Hedi Formation, which is considered to be Sharamurunian based on an abundance of small mammal fossils.

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云南丽江盆地中始新世奇蹄类化石再研究及*Diplolophodon*的修订

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摘要：云南西部丽江盆地中始新世丽江组中的哺乳动物群以奇蹄类占据优势，之前已经报道了13个种，丽江动物群的时代被认为从伊尔丁曼哈期延续到沙拉木伦期。重新研究了丽江盆地的部分奇蹄类化石，认为*Rhodopagus yunnanensis*是*Lijiangia zhangi*

的次同物异名，而后者具有和*Lophiohippus*相似的特征，所以将*Lijiangia*置于古兽科(Palaeotheriidae)的Anchilophini, 而不是最初有疑问地归入的蹄齿犀科(Hyracodontidae)。*Lunania*也代表了一类和*Paranchilophus*相似的古兽而不是爪兽；如果*Lophiohippus*的正型标本代表了*Lunania*的上臼齿，那么*Lophiohippus*是*Lunania*的次同物异名。通过对戴氏貘科(Deperetellidae) *Diplolophodon*的厘定，认为该属包括了3个种：*D. similis*, *D. lunanensis* 和*D. xiangshanensis* (新组合), 其中丽江盆地的*Teleolophus xiangshanensis*应归入到*Diplolophodon xiangshanensis*。丽江盆地的奇蹄类化石组合和垣曲盆地河堤组任村段的奇蹄类化石相似性最高，且丽江动物群的时代应限于中始新世沙拉木伦期。

关键词：云南丽江盆地，中始新世，Anchilophini, *Lijiangia*, Deperetellidae, *Diplolophodon*

References

Bai B, 2017. Eocene Pachynolophinae (Perissodactyla, Palaeotheriidae) from China, and their palaeobiogeographical implications. Palaeontology, 60(6): 837–852

Bai B, Wang Y Q, Li Q et al., 2018. Biostratigraphy and diversity of Paleogene perissodactyls from the Erlian Basin of Inner Mongolia, China. Am Mus Novit, 3914: 1–60

Bai B, Meng J, Zhang C et al., 2020. The origin of Rhinocerotoidea and phylogeny of Ceratomorpha (Mammalia, Perissodactyla). Commun Biol, 3: 1–16, https://doi.org/10.1038/s42003-020-01205-8

Chow M C, 1957. On some Eocene and Oligocene mammals from Kwangsi and Yunnan. Vert PalAsiat, 1(3): 201–214

Chow M C, 1962. A new species of primitive chalicothere from the Tertiary of Lunan, Yunnan. Vert PalAsiat, 6(3): 219–224

Chow M C, Zhang Y P, Ding S Y, 1974. Some Early Tertiary Perissodactyla from Lunan Basin, E. Yunnan. Vert PalAsiat, 12(4): 262–273

Colbert E H, 1938. Fossil mammals from Burma in the American Museum of Natural History. Bull Am Mus Nat Hist, 74(6): 255–436

Dashzeveg D, Hooker J J, 1997. New ceratomorph perissodactyls (Mammalia) from the Middle and Late Eocene of Mongolia: their implications for phylogeny and dating. Zool J Linn Soc, 120: 105–138

Ding S Y, Zheng J J, Zhang Y P et al., 1977. Age and characteristic of Liuniu and Dongjun faunas, Bose Basin of Guangxi. Vert PalAsiat, 15(1): 35–44

Hooker J J, 1989. Character polarities in Early Eocene perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. In: Prothero D R, Schoch R M eds. The Evolution of Perissodactyls. New York: Oxford University Press. 79–101

Hooker J J, 1994. The beginning of the equoid radiation. Zool J Linn Soc, 112: 29–63

Huang X S, 1999. Middle Eocene mammals of Lijiang Basin, Yunnan. In: Wang Y Q, Deng T eds. Proceeding of the 17th Annual Meeting of the Chinese Society of Vertebrate Paleontology. Beijing: China Ocean Press. 125–138

Huang X S, 2002. New emoropid (Mammalia, Perissodactyla) remains from the Middle Eocene of Yuanqu Basin. Vert PalAsiat, 40(4): 286–290

Huang X S, Qi T, 1982. Notes on Late Eocene tapiroids from the Lunan Basin, eastern Yunnan. Vert PalAsiat, 20(4): 315–326

Huang X S, Wang J W, 2001. New materials of tapiroid and rhinocerotoid remains (Mammalia, Perissodactyla) from the Middle Eocene of Yuanqu Basin, Central China. Vert PalAsiat, 39(3): 197–203

Huang X S, Wang J W, Tong Y S, 2001. Recent progress on study of Eocene mammals in Yuanqu Basin. Vert PalAsiat, 39(2): 88–97

Jin H Y, Seo K-s, 2001. A new species of *Diplolophodon* (Perissodactyla: Tapiroidea) from Yunnan, China. Geosci J, 5(2): 153–157

Lee Y Y, Lee J, Chu S, 1935. Geology of the Nanjing Hills. Mem Natl Inst Geol, Acad Sin, 11: 1–379

Misch P, 1945. Remarks on the tectonic history of Yunnan, with special reference to its relations to the type of the young orogenic deformation. Bull Geol Soc China, 25(1): 47–153

Radinsky L B, 1965. Early Tertiary Tapiroidea of Asia. Bull Am Mus Nat Hist, 129(2): 181–264

Remy J A, 2012. Révision systématique des Anchilophini (Palaeotheriidae, Perissodactyla, Mammalia). Palaeovertebrata, 37(1-3): 1–165

Russell D E, Zhai R J, 1987. The Palaeogene of Asia: mammals and stratigraphy. Mém Mus Natl Hist Nat, Ser C, 52: 1–488

Shi R, 1989. Late Eocene mammalian fauna of Huangzhuang, Qufu, Shandong. Vert PalAsiat, 27(2): 87–102

Tsubamoto T, Holroyd P A, Takai M et al., 2000. Upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, Myanmar. Paleontol Res, 4(3): 183–189

Tsubamoto T, Egi N, Takai M et al., 2005. Middle Eocene ungulate mammals from Myanmar: a review with description of new specimens. Acta Palaeontol Pol, 50(1): 117–138

Wang H B, Bai B, Gao F et al., 2013. New eggysodontid (Mammalia, Perissodactyla) material from the Paleogene of the Guangnan Basin, Yunnan Province, China. Vert PalAsiat, 51(4): 305–320

Wang Y Q, Li Q, Bai B et al., 2021. Lithostratigraphic subdivision and correlation of the Paleogene in China. J Stratigr, 45(3): 402–425

Young C C, 1937. An Early Tertiary vertebrate fauna from Yuanchü. Bull Geol Soc China, 17(3-4): 413–438

Zdansky O, 1930. Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. Palaeont Sin, Ser C, 6(2): 1–87

Zhang Y P, You Y Z, Ji H X et al., 1978. Cenozoic stratigraphy of Yunnan. Prof Pap Stratigr Palaeont, 7: 1–21

Zhao G G, 1965. Preliminary observations оп the Cenozoic deposition and structure in the Lijiang-Dali region of northwestern Yunnan. Geol Rev, 23(5): 345–358

Zheng J J, Tang Y J, Zhai R J et al., 1978. Early Tertiary strata of Lunan Basin, Yunnan. Prof Pap Stratigr Palaeont, 7: 22–29

Zheng J J, He X X, Liu S W et al., 1999. Stratigraphical Lexicon of China—Tertiary System. Beijing: Geological Publishing House. I–163

Zong G F, Chen W Y, Huang X S et al. 1996. Cenezoic Mammals and Environment of Hengduan Mountains Region. Beijing: China Ocean Press. 1–279